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AMERICAN CRETACEOUS INSECTIVORES

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INTRODUCTION

A Mesozoic mammal was discovered in 1764. After the passage of 187 years, knowledge of the Mesozoic Mammalia is still extremely unsatisfactory. There are few important paleontological topics about which we know less than we do about the whole first half, or more, of the history of the class to which we and the most familiar of our associated animals belong. Even the few bits of information that have been gleaned are still on many points highly uncertain as to interpretations and significance. We do not, for instance, know anything whatever about late Cretaceous mammals in Europe, Africa, South America, or Australia, and the real variety and composition of the known Cretaceous North American and Asiatic mammalian faunas are not really understood.

When Marsh (1889a, 1889b, 1892) described the first considerable collection of Cretaceous mammals, from what is now called the Lance formation of Wyoming, he recognized that some of these were multituberculates or Allotheria, while others were considered marsupials more or less near the living possums in affinities, and some were believed probably to be insectivores. Osborn (e.g., 1891) was violently critical of Marsh's work on this subject (as well as on most others). He quickly concluded that the known specimens were really indeterminate as to affinities, whether marsupial or placental. Aside from the multituberculates, he compared them with placentals rather than marsupials. Several of them were later explicitly considered (Osborn, 1898) as "capable of giving origin to the teeth of the Amblypoda" (i.e., some condylarths and some pantodonts, both placental groups). Still later (e.g., 1907) he concluded that marsupials were defi-

nitely present, as Marsh had said, but he still considered it possible that Insectivora, Carnivora, and ancestors of ancient types of Ungulata were also present.

Although Osborn consistently stressed the great difference between known Jurassic and late Cretaceous mammals and insisted that the latter were already essentially Tertiary in type, his work initiated another point of confusion on this subject which still persists in some textbooks. He called the Jurassic Pantotheria "Trituberculata" or "trituberculates" and applied the same term to all the possible marsupials or placentals from the late Cretaceous. It thus appeared that the same group or order of mammals was considered present in the Jurassic and the Cretaceous as distinct from the Tertiary orders. This has been taken at face value by various students, although it is not the case and was not Osborn's opinion.

In 1916 Matthew described the first Cretaceous therian (= marsupial or placental) mammal, *Eodelphis*, to be known by material such that no doubt as to its affinities was possible. This form is certainly a marsupial and quite close to the living opossum, *Didelphis*. Matthew then concluded that all the other known Cretaceous therians were probably also marsupials or, at least, that "there was not and is not any valid evidence for placing any of them in the placental group" (Matthew, 1916). This conclusion, justified on the basis of materials then before Matthew, fitted in with a widespread idea that ancient mammals *should* be marsupials. This a priori judgment had such prejudicial force that it continued to be followed by a number of writers even after the demonstration that placentals do occur in the Cretaceous beyond any doubt whatsoever.

This demonstration was made in 1926 on the basis of specimens found in the late Cretaceous Djadokhta formation of Mongolia (Gregory and Simpson, 1926). The possible presence of placentals in the American Cretaceous faunas remained open, or became again open, after this discovery. Shortly thereafter, I (Simpson, 1927, 1929a) suggested that isolated teeth, to which the name *Gypsonictops* was applied, almost certainly did represent placental mammals in the Lance and Hell Creek formations. With greater doubt, it was suggested that Marsh might have been right in thinking that some of his genera, particularly *Telacodon* and *Batodon*, were also placentals. (It was by this time clear, how-

ever, that certain other forms, notably *Pediomys*, once considered possible placentals by Marsh, were marsupials.)

As of 1929, the situation regarding known Cretaceous therian mammals was thus as follows:

Such mammals were known by a small number of relatively good specimens from the Djadokhta of Asia and by large numbers of very fragmentary specimens from the Lance and equivalents of North America, plus a few specimens of slightly earlier age from Canada. No therians were known from Cretaceous strata anywhere outside of one spot in Asia and one broader region in North America.[1] The known Asiatic therians were all clearly demonstrated to be placentals, of the Order Insectivora. Of the North American forms, one genus, *Gypsonictops*, was established as an insectivore, and two or three others, ill defined, were suspected of being insectivores. The few pre-Lance therians and some Lance forms were demonstrated to be marsupials. The great majority of the numerous poorly known other Lance therians were believed also to be marsupials belonging in or near the family Didelphidae.

There the matter has rested for more than 20 years. Now the discovery of some new Cretaceous specimens, reconsideration of materials in older collections, and increased knowledge of Tertiary insectivores lead to some modification of the earlier conclusions. The general picture of a late Cretaceous North American mammalian fauna as consisting of abundant multituberculates, abundant opossum-like marsupials, and some insectivores is not materially modified. The suggestion is, however, made that the placental, insectivore element in this fauna was probably considerably larger and more varied than has been supposed. This modification of opinion still lacks full proof, but its probability has interest and importance. This is only superficially a return to the early view of Osborn, who implied, at least, a large and varied placental element in this fauna, because his evidence was mostly incorrect. Most of his specimens are still believed to be marsupials. It was in large part the discovery of the more probable affinities of those specimens that led to former too extreme views as to the preponderance of marsupials, an over-compensation of opinion which the present notes are designed to correct.

[1] In 1929 it was still commonly believed, although I had questioned the belief, that Cretaceous therians were known from South America. It was later established beyond much question that this was an error (Simpson, 1932).

I am particularly indebted to Dr. P. O. McGrew, University of Wyoming, for turning over to me important new specimens found by him and his students and for giving a clue which led to correction of an early blunder by me (as related hereunder). Drs. J. T. Gregory, Yale University, and C. L. Gazin, United States National Museum, kindly permitted and facilitated restudy of specimens in the Marsh collections in their respective care. Mr. J. Le R. Kay, Carnegie Museum, made possible restudy of the type of *Euangelistes petersoni*. Mr. D. B. Kitts assisted with some measurements and compilation. The illustrations were made by Mr. John Le Grand.

The following abbreviations indicate depositories of specimens described.

A.M.N.H., the American Museum of Natural History
C.M., Carnegie Museum, Pittsburgh
U.S.N.M., United States National Museum
U.W., University of Wyoming
Y.P.M., Peabody Museum, Yale University

When available, accession or locality data are given for Marsh specimens. These localities are listed and discussed in Lull (1915).

UPPER TEETH

Upper premolars and molars of insectivores from the Lance were referred by Marsh (1892) to *Batodon* and *Telacodon*, genera based on lower jaw fragments, with the comment that "their exact relation to each other is, of course, uncertain." The upper teeth belonged to closely similar animals, and Marsh's reasons for referring some to *Batodon* and others (a majority) to *Telacodon* were not explicit. Recognizing that these teeth might belong to a genus named from lower teeth, I nevertheless pointed out that correct generic association on this basis was impossible and felt that the undoubted insectivore upper teeth needed a name for convenient discussion. I therefore placed them all under a then new generic name, *Gypsonictops* (Simpson, 1927, 1929a). No noteworthy change in these previous conclusions is now necessary or addition possible, but some notes on variation and an attempt at reconstruction are to be presented.

The following upper premolars have been reëxamined:

Y.P.M. No. 13651. Right upper premolar in fragment of jaw. Accessioned

May, 1891, from Lusk, Wyoming. Figured, Marsh (1891, pl. 9, fig. 2) as a premolar of *Telacodon laevis;* Simpson (1929a, fig. 53, upper right; pl. 32, fig. 6) as *Gypsonictops hypoconus.*

Y.P.M. No. 13653. Left upper premolar. Accessioned August, 1889, from Hat Creek, Wyoming. Figured, Marsh (1891, pl. 11, fig. 2) as a molar of *Batodon tenuis.*

U.S.N.M. No. 5040. Right upper premolar. Quarry 9, Lance Creek, Converse County, Wyoming. Not published.

U.S.N.M. No. 5042. Left upper premolar. Quarry 9, Lance Creek, Converse County, Wyoming. Not published.

A.M.N.H. No. 2225. Left upper premolar. Lance Creek, Converse County, Wyoming. Figured, Osborn (1893, pl. 8, fig. G) without determination.

These specimens vary slightly in size, proportions, and relative prominence of the various cusps, styles, and cingula, but all are fundamentally so similar that they could well be homologous teeth of a single species. The facts that they are all so nearly alike and that no other partly molariform upper premolars have been found are suggestive evidence, at least, that these teeth are P^4 of the commonest Lance insectivore and that P^{1-3} were simple, not incipiently molariform, teeth. Simple premolars are, in fact, present in the collections, but in the absence of any association their identification seems hopeless. Possibility that the listed premolars are P^3 rather than P^4 is not excluded, but is unlikely (see below).

In lieu of detailed description and to supplement inadequate previous illustration, one of the best preserved of these teeth is figured (fig. 1).

Upper molars are relatively common in the Lance and Hell Creek. More than 20 specimens have been studied in the Yale, United States National Museum, American Museum, and Wyoming collections. It seems unnecessary to list all of these, but the following are of special interest:

Y.P.M. No. 13662. Right M^1 or M^2, probably M^2. Peterson Quarry, Wyoming. Type of *Gypsonictops hypoconus.* Figured, Simpson (1929a, fig. 53, "Typical Molar"; pl. 32, figs. 3–5).

U.S.N.M. No. 5043. Right M^1 or M^2, probably M^2. Lance Creek, Converse County, Wyoming.

U.S.N.M. No. 5044. Left M^1 or M^2. Lance Creek, Converse County, Wyoming.

A.M.N.H. No. 39595. Right M^1. W 1/2, Sect. 23, T38N, R64W, Wyoming. Collected by the University of Wyoming.

U.W. No. 518. Left M^1 or M^2. SE 1/4, Sect. 21, T38N, R64W, Wyoming.

Y.P.M. No. 13667d. Right M^3. Accessioned August, 1891, from Lusk, Wyoming. Figured, Simpson (1929a, fig. 53, upper left).

Among the teeth most suggestive of M^2 there are at least two rather distinct forms. The more common type is represented by Y.P.M. No. 13662, type of *Gypsonictops hypoconus*, or by U.S. N.M. No. 5043. U.W. No. 518 has the same general structure but it is larger, less transverse (or less compressed anteroposteriorly), and has the parastyle projecting less far buccally.

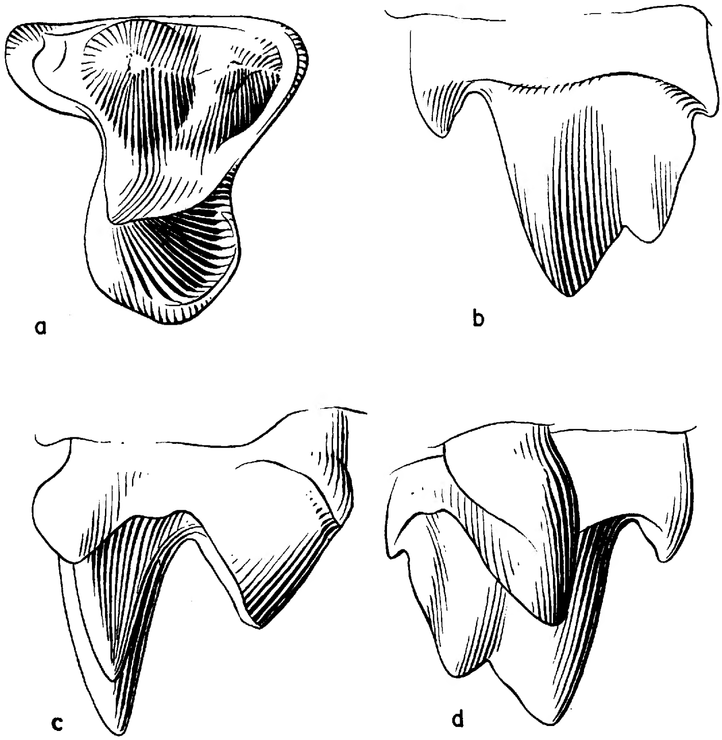

FIG. 1. P^4 of a Cretaceous insectivore, cf. *Gypsonictops*. U.S.N.M. No. 5042. A. Crown view. B. External view. C. Posterior view. D. Internal view. × 17.

A.M.N.H. No. 39595, presumed M^1, is also smaller than U.W. No. 518, but otherwise differs decidedly from the *G. hypoconus* type, being less transverse, with less buccal parastyle and more oblique outer border.

Aside from unquestionable premolars (all essentially alike) and unquestionable M^3, there are thus at least three different sorts of molariform teeth in the collections, which are from scattered localities and various horizons within the Lance formation. (See fig. 2.) Possibilities are: (a) that one of these types represents a

fully molariform P^4, the recognized premolars being P^3, (b) that one is a fully molariform dm^4, and (c) that two or more species or closely allied genera are present. Any one or simultaneously

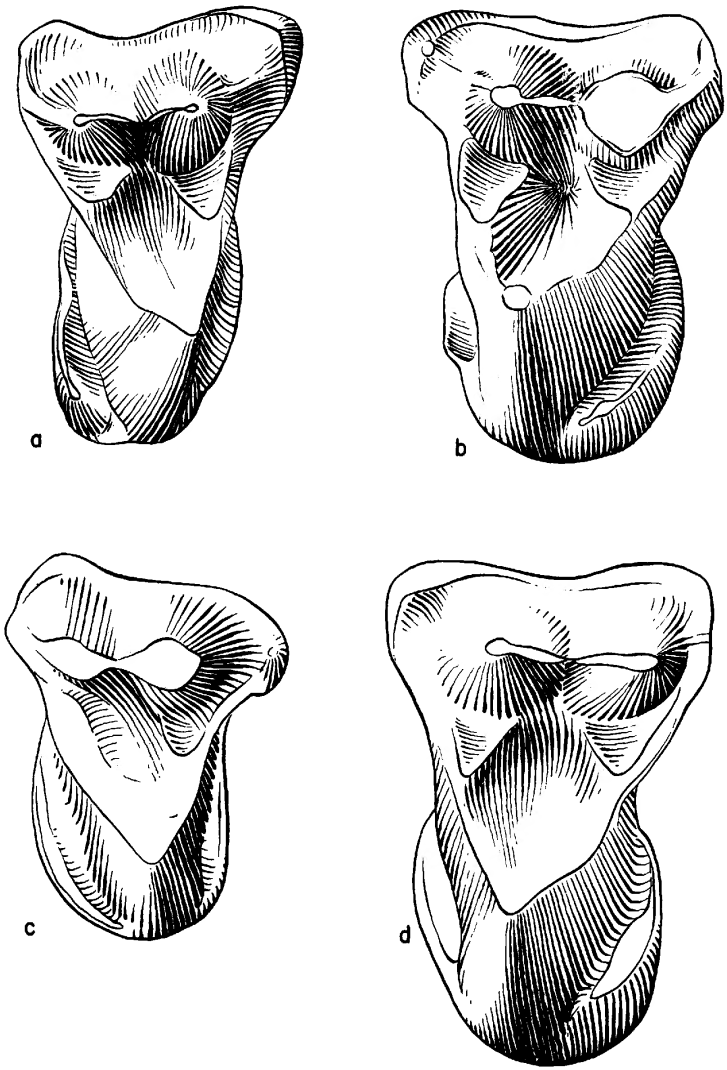

FIG. 2. Upper molars of Cretaceous insectivores, cf. *Gypsonictops*. A. U.S.N.M. No. 5043. B. U.S.N.M. No. 5044. C. A.M.N.H. No. 39595. D. U.W. No. 518. × 17.

more than one of these possibilities may well prove to be correct, but the first is improbable on present evidence. A *completely* molariform P^4 is improbable in such an early insectivore. If the

teeth here tentatively identified as P^4 are really P^3, then P^3 is decidedly more molariform than in any possibly allied form, even among much later and generally more advanced forms, a strong improbability. U.W. No. 518 is distinctive not only in structure but also in size, being perhaps too large to belong to the same species as the majority of specimens, whatever its homologies may be.

It is, however, probable that these teeth are not correctly assorted simply by referring U.W. No. 518 to a different species. There is a very strong probability that the majority of the teeth, those varying but little from the *G. hypoconus* type, include both M^1 and M^2. Test by chi-squared of the hypothesis that these are all M^2 and that A.M.N.H. No. 39595 is M^1 of the same form shows that this hypothesis is prohibitively improbable (P far less than .01) unless the chances of collecting M^2 of this form were much greater than those of collecting M^1, an unlikely condition. There is also sufficient variation in these teeth for them to represent both M^1 and M^2. For instance, U.S.N.M. No. 5044 has the parastyle more anterior, less buccal, than the otherwise similar U.S.N.M. No. 5043, and these could be M^1 and M^2 of the same species. But A.M.N.H. No. 39595 is sufficiently unlike either U.S.N.M. No. 5044 or No. 5043 as to make it improbable that they are homologous teeth of the same species. A.M.N.H. No. 39595 could be dm^4, but this is improbable. It is a stout, well-rooted tooth with crown relatively as high as the other specimens and enamel similarly stained. (The enamel of deciduous teeth commonly stains differently, usually less darkly, than that of permanent teeth, and deciduous teeth are almost always distinctly lower crowned.)

These considerations all underline the probability that the isolated upper teeth represent at least two and perhaps three distinct species or genera, although the structural similarities suggest that the groups present are closely allied. It is impossible to combine teeth into a composite representing, with any proper degree of accuracy, a single species. In figure 3 I have, nevertheless, attempted a synthetic, hypothetical reconstruction of P^4–M^3 of a member of this general group of insectivores. Because identification of A.M.N.H. No. 39595 as M^1 is as secure as any attempt to differentiate M^1 and M^2 and because this tooth is of appropriate size for occlusion with *Euangelistes* (see below), I have started with it. The other teeth in the reconstruction are not drawings of actual specimens and are hypothetical to that extent, but they

embody the structural details of real specimens, adjusted in size and proportions to A.M.N.H. No. 39595 as M^1. Also involved is the probable, but uncertain, conclusion that the known premolars are P^4. It is emphasized that this reconstruction does not represent a known genus or species and that it may prove to be incorrect in some essentials. Nevertheless it represents a reasonable hypothesis as to the general nature of the dentition in the group of Cretaceous insectivores to which *Gypsonictops* belongs, and on this basis may be used with due reservations in exploration of the possible nature and affinities of that group.

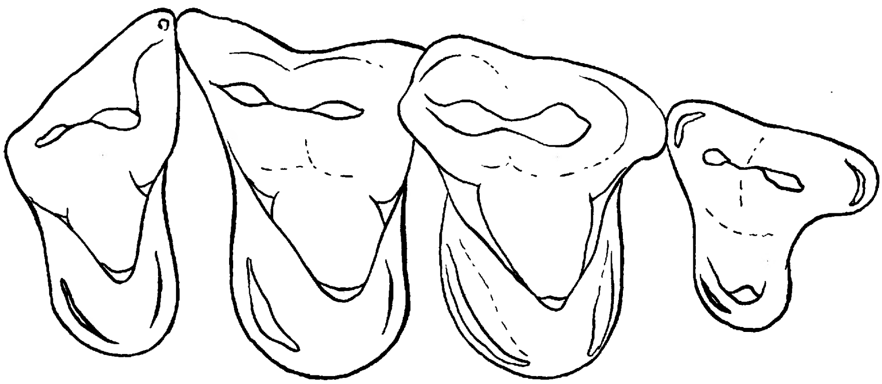

FIG. 3. Hypothetical reconstruction of P^4–M^3 of a Cretaceous insectivore, cf. *Gypsonictops*. M^1 is based on A.M.N.H. No. 39595. The other teeth are based on specimens but are diagrams adjusted to M^1 and are not portraits of particular specimens. × 14.

LOWER TEETH

As previously noted (Simpson, 1929a) *Telacodon laevis* Marsh, 1892, and *Batodon tenuis* Marsh, 1892, are probably insectivores. Both are based on anterior fragments of mandibles with premolars but no molars. The two are similar to each other but are probably correctly placed as different genera. The canine is more enlarged in *Batodon*, and *Telacodon* may have had a more enlarged incisor, although reëxamination of the specimens leads me to think that these differences are less certain, or less marked, than I suggested in 1929. The apparent P_4, preserved in both specimens and probable but not quite certain as to homologies, is simple in both cases and not at all molariform. This makes it rather improbable that either *Telacodon* or *Batodon* is congeneric with the submolariform P^4 described above and probably belonging to *Gypsonictops*,

and makes it impossible for either to be congeneric with *Euangelistes* (see below) unless the apparent P_4's are in fact more anterior teeth.

Telacodon praestans Marsh, 1892, was based on a lower jaw fragment with the last two molars. Reëxamination confirms my previous (1929) conclusion that this is a small didelphid and that it therefore probably has nothing to do with *Telacodon,* which seems to be an insectivore. An isolated lower molar, now U.S. N.M. No. 2886, was also figured as *Telacodon praestans* by Marsh (1892, pl. 11, fig. 8). It is a peculiar tooth wholly uncertain as to affinities.

Marsh (1892, pl. 10, fig. 6) also figured a lower jaw fragment with the last two molars and referred this to *Batodon tenuis.* This specimen, now Y.P.M. No. 10685, seems to be a small didelphid and probably has nothing to do with *Batodon,* although the possibility is not wholly excluded.

Lower molars of American Cretaceous insectivores have not hitherto been surely identified, although it might have been taken as practically certain that they are present in the known collections. In fact, I had myself examined, described, and figured a considerable number of these teeth without recognizing them as insectivores. It was Dr. Paul O. McGrew, on the basis of a new specimen found by him, who first suggested that certain supposedly marsupial teeth are in fact the long-missing insectivore lower molars. I am much indebted to him for this clue and, particularly, for his courteous insistence that my serious blunder be corrected by myself.

It now appears that *Euangelistes petersoni* Simpson, 1929, is an insectivore. The type, C.M. No. 11,657, is part of a left lower jaw with P_3–M_2.[1] My insistence (Simpson, 1929b) that the specimen was marsupial was based on belief that it has four molars. In fact, the tooth now identified as P_4, then considered M_1, is almost molariform, had erupted precisely to the level of a molar, and is like the molars in enamel color and fossilization. The fact that the preceding tooth is not at all molariform also

[1] As found and originally studied by me, the specimen also had M_3. After my study was completed and the specimen returned to the Carnegie Museum, it was shattered while being drawn. Dr. O. A. Peterson managed to restore most of the fragments, but M_3 was lost. M_3 had not yet been drawn, so that all we know of this tooth is my earlier note that it was generally similar to M_2 but with a more projecting hypoconulid.

weighed against considering this a molarized premolar. It therefore fitted in with my bias, of that period, arising from attempts to prove that most of the small "trituberculates" of the Lance are didelphids, a point then in doubt that I was able firmly to establish but that blinded me when I dealt with this specimen and its allies.

The tooth in question now seems quite surely to be a molarized P_4. It is not entirely molariform. It has no protolophid or distinct to vestigial paraconid, as on the molars. A sort of small pseudoparaconid, low on the crown, is supplied by a style-like prominence or shelf at the lingual end of the anterior cingulum. The metaconid is large, as on the molars, but the trigonid is peculiarly bicuspid and is shorter anteroposteriorly than on the molars. The talonid is narrower than on M_{1-2}. Similarly molariform P_4's are not uncommon among insectivores. On reexamination it also appears, although not very clearly, that this tooth is slightly less worn than the following tooth, a condition normal for P_4–M_1 and not for M_{1-2}.

Lower molars of insectivores and primitive marsupials are often extraordinarily similar, but there is one fairly constant difference: in didelphids the hypoconulid is normally lingual in position, almost twinned with the entoconid, while in insectivores it is usually medial and not distinctly more closely associated with the entoconid than with the hypoconid. This character is obscured by wear on the type of *E. petersoni,* but isolated, unworn teeth surely congeneric clearly have the insectivore and not the didelphid sort of hypoconulid.

Recognition that *Euangelistes* is an insectivore and resurvey of the collections show that insectivore P_4's and lower molars are fairly common in the Lance, at least 20 isolated teeth being present in the Yale, United States National Museum, and American Museum collections. The abundance is about the same as for recognized insectivore P^4's and upper molars.

The following previously figured specimens are now identified as belonging to *Euangelistes:*

Y.P.M. No. 10697b. Right P_4. Quarry 5, Wyoming. Figured, Marsh (1892, pl. 10, fig. 5) as *Cimolestes incisus,* and by Simpson (1929, fig. 50, 9) as "Type 9" of supposed didelphid lower molars.

Y.P.M., no catalogue number. Left lower molar. Accessioned August, 1891, from Lusk, Wyoming. Figured, Simpson (1929, fig. 50, 7) as "Type 7" of supposed didelphid lower molars.

The original of Marsh (1892, pl. 11, fig. 3), a right lower molar

referred by Marsh to *Batodon tenuis*, may also belong to *Euangelistes*, but the specimen has not been reëxamined.

Marsh's reference of Y.P.M. No. 10697b to *Cimolestes incisus* reflects a real resemblance, both in size and structure, between molars of *Euangelistes* and of *Cimolestes*. This is not an identity, however, and the genera seem to be distinct. *Cimolestes* may possibly be another insectivore, but it still seems likely that it is a didelphid.

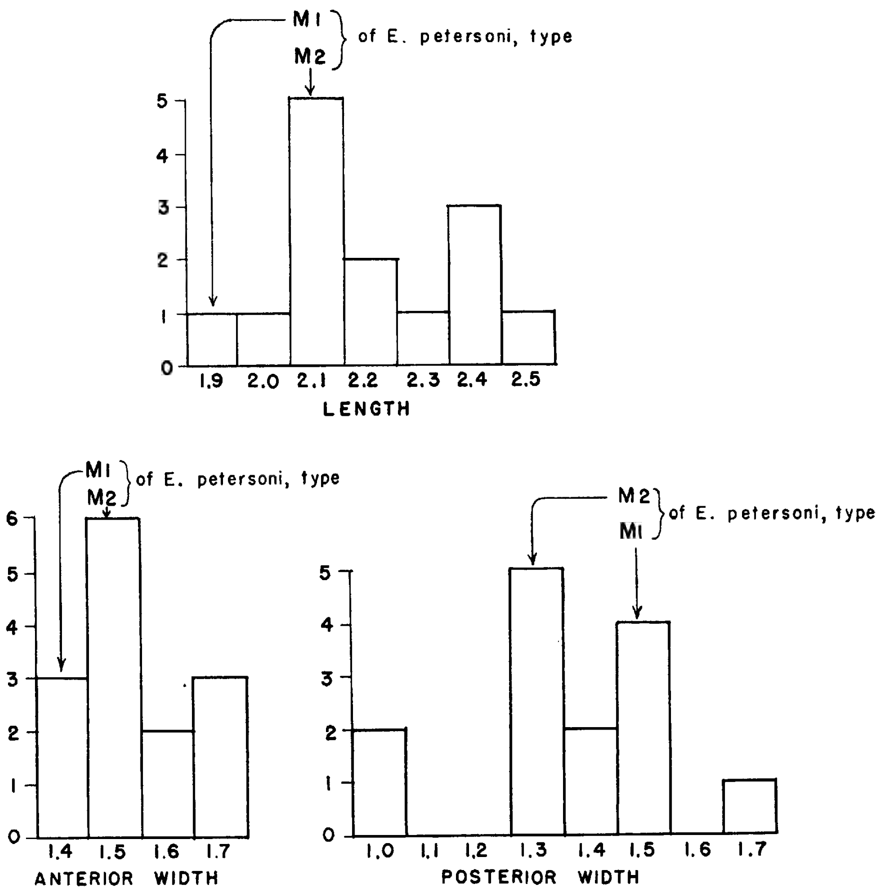

FIG. 4. Frequency histograms of dimensions of lower molars, cf. *Euangelistes*.

Measurements of 12 isolated lower molars in the United States National Museum collection and of the two preserved molars of the type of *E. petersoni* have been taken, and the results are graphically summarized in figure 4. M_1, M_2, and M_3 seem to inter-

grade in all dimensions, and attempts to sort the teeth by size, proportions, or morphology have not been successful. The most nearly clear distinction seems to be in the absolute and relative posterior width (i.e., across the talonid). On M_1 this is nearly, or quite, equal to the anterior width (across the trigonid), on M_2 it is generally less, and on teeth tentatively identified as M_3 it is decidedly less, to as little as two-thirds of the anterior width. The teeth with unusually narrow posterior width, or high ratio of anterior to posterior width, also have more projecting hypoconulids, a usual character of M_3.

The irregular distributions, large ranges, and some possible but here very uncertain excess of teeth in the range of M_2 (analogous to the clearer excess of apparent M^2 among upper teeth) suggest some taxonomic heterogeneity among these lower molars. The evidence is, however, wholly inadequate, and all may possibly be of one species.

The type of *Euangelistes petersoni* gives the series P_3–M_2 in association, and M_3 can be added from an isolated specimen almost certainly M_3 of this species to complete a reconstruction of most of the lower cheek dentition (fig. 5).

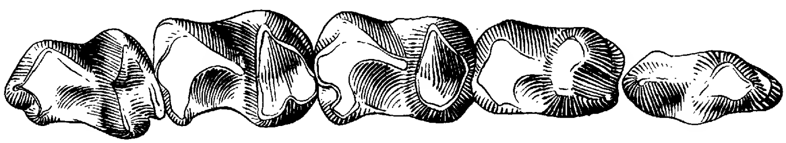

FIG. 5. P_3–M_3 of *Euangelistes*. P_3–M_2 are correctly associated and are drawn from C.M. No. 11657. M_3 is hypothetically added and is drawn from U.S.N.M. No. 5107. × 10.

ASSOCIATION AND VARIETY

Evidence has been adduced that the upper molars of Lance insectivores include more than one form, although all are similar in general character. The hypothetical reconstruction of P^4–M^3 based on isolated upper teeth occludes reasonably well with the reconstructed P_3–M_3 of *Euangelistes petersoni* (fig. 7). In view of doubts as to how many species or closely related genera may be involved here, this does not demonstrate synonymy of *Gypsonictops* and *Euangelistes*. As a formal device separate names may be retained for the upper and lower dentitions, even though it is certain that some among them are in fact upper and lower teeth of the same genus. The situation is further complicated and

variety in the insectivore fauna further indicated by the fact that *Batodon* and *Telacodon*, if correctly interpreted, cannot be synony-

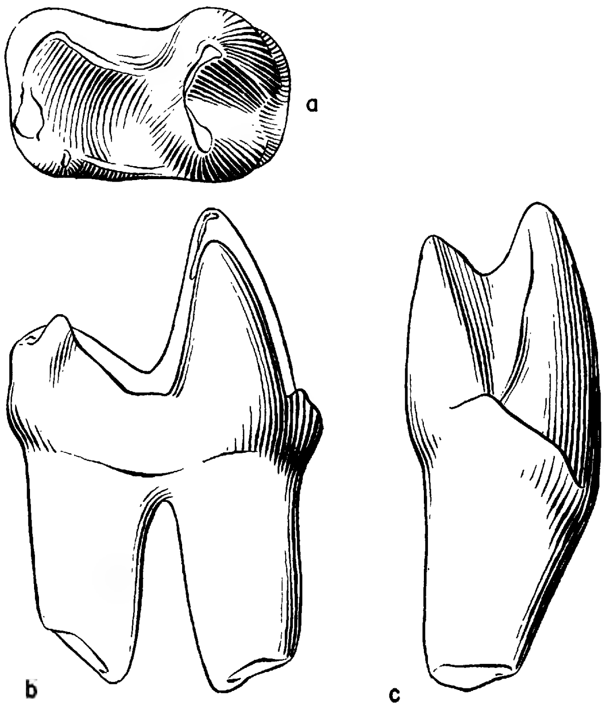

FIG. 6. P_4 of *Euangelistes*. A.M.N.H. No. 39581. A. Crown view. B. Internal view. C. Anterior view. X 17.

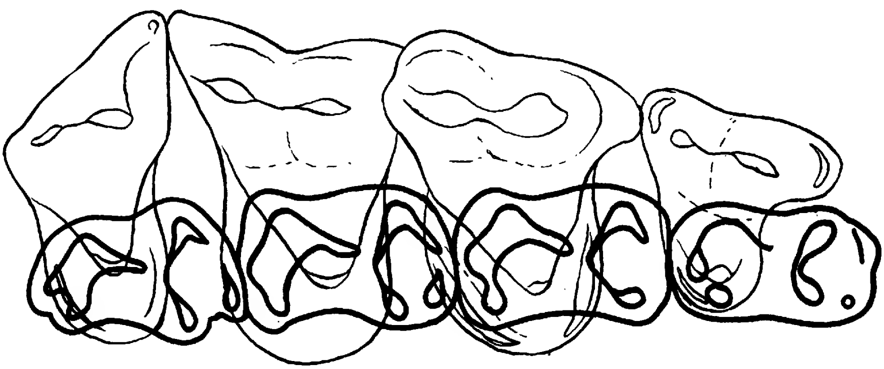

FIG. 7. Occlusion of hypothetical P^4–M^3 (as in fig. 3), cf. *Gypsonictops*, and P_4–M_3 of *Euangelistes*. × 14.

mous with *Euangelistes*. Molars of these genera have not been identified. Alternatives are that they (1) are absent in the col-

lections, (2) are so similar to *Euangelistes* that they have not been separated, in spite of the apparent difference in P_4, or (3) are among the small molars still not distinguished from those of didelphids.

AFFINITIES

Pending further evidence on these problems, combination of the reconstructed *Gypsonictops*-like upper dentition and the *Euangelistes* lower dentition, even though frankly hypothetical in part, gives a type of cheek-tooth structure and occlusion which has some probability of approximating a reality and the affinities of which can be considered on this basis. Due warning has been insistently given in this paper and the reader will appreciate the fact that this discussion would be invalidated by the quite possible discovery that the animal to which it refers did not really exist. The existence of something like it is, nevertheless, sufficiently probable to give the discussion some value in view of the great importance and rarity of these earliest insectivores.

Gypsonictops has hitherto been tentatively referred to the Leptictidae (see Simpson, 1929a). The structure of M^1 or M^2 is, indeed, leptictid, but the hypothetically associated dentition is less so, and there are several other insectivore families in which similar molars occur, especially Zalambdalestidae and Erinaceidae. There are also some similarities to a few other groups, such as the Pantolestidae, which nevertheless are more distant and have various peculiarities apparently precluding close relationship to our Cretaceous form.

The Asiatic genus *Zalambdalestes*, also a Cretaceous insectivore, have already diverged considerably from this American insectivore. They cannot be on the same line of descent and may not have been more closely related than all insectivores were in the Cretaceous (which, presumably, was a rather close relationship in spite of great later divergence of various lines). In *Zalambdalestes* (see Gregory and Simpson, 1926; Simpson, 1928) P^3 was partly molariform and P^4 almost fully so in shape but with metacone not differentiated. The molars lack hypocones. P_4 has an elongate trigonid with a paraconid.

Even the earliest unquestioned leptictids (middle Paleocene) have P^4_4 distinctly more molariform than in the synthetic Cretaceous form. This could, of course, be merely a progressive character, consonant with later age, but the peculiar structure of

P^4 and, more particularly, of P_4 in the Cretaceous form certainly does not point towards the stereotyped leptictid structure of these teeth. The leptictids also usually, but not quite invariably, have the paracone and metacone more buccal, or the shelf external to them narrower.

Resemblance to true, typical or undoubted Erinaceidae is not so close as to Leptictidae, but there is a special resemblance to two American Oligocene genera of questioned affinities: *Metacodon* Clark, 1936, and *Ankylodon* Patterson and McGrew, 1937. Clark (1937) referred *Metacodon* to the Leptictidae. Patterson and McGrew (1937) placed it and its ally *Ankylodon* in the Erinaceidae. Clark (1939) agreed that this is possible, but pointed out that *Metacodon* is distant from *Proterix*, a contemporaneous form more definitely erinaceid in structure. Butler (1948) proposed a family Metacodontidae "to include the genera *Metacodon*, *Meterix* and *Plesiosorex* which, although they may eventually prove to be related to the Erinaceidae, are too imperfectly known to be placed with certainty in that family." The offhand proposal of an undefined new family on such a basis is hardly to be commended. The system would rapidly become chaotic if a family of its own were provided for every genus that cannot be placed with certainty in a family to which it may nevertheless belong, and after all there are already not only one but at least two previously named families to which *Metacodon* might eventually prove to belong.

Yet this action at least emphasizes the fact that *Metacodon* is not a typical or unquestionable erinaceid. Wherever it may be placed, *Ankylodon* (not listed in the Metacodontidae by Butler) probably belongs with it. *Meterix* and *Plesiosorex* probably do not; at least, the published descriptions (especially Hall, 1929, and Viret, 1940) do not seem to me to show any special resemblance to *Metacodon*. It is quite possible that some of the less well-known Paleocene and Eocene genera, especially among those currently referred to the Leptictidae, will prove to be allies of *Metacodon*, but a review of these is not possible in the present paper.

The upper molars of *Metacodon* are basically similar to those of the synthetic Cretaceous genus, with subequal paracone and metacone, wide buccal cingulum, crests from protocone to parastyle and metastyle (a non-erinaceid character, as Butler notes, and one suggestive of the Leptictidae), a small anterior cingulum, and

a low, cingulum-like hypocone. The buccal shelf is a little wider than in most of the Cretaceous teeth, the metastyle more prominent on M^1, and the conules are small or absent (but they are readily obscured by wear in such teeth). P^4 is rather similar in degree of molarization, but the outer part is more oblique in *Metacodon,* and there is no separate metacone. In the Cretaceous P^4's the metacone is distinct, although small and not well separated from the paracone. This character was strongly emphasized by Patterson and McGrew in moving *Metacodon* from the Leptictidae to the Erinaceidae. Probably it excludes the Cretaceous form from the direct ancestry of *Metacodon,* but it does not seem to me to exclude rather close relationship. The Cretaceous P^4 is about as much like *Metacodon* as like typical leptictids, and, indeed, as a rather slight variation it tends to some extent to fill the apparent gap in structural range for this tooth among the primitive, descriptively erinaceomorph dentitions.

P_3 in *Metacodon* is relatively smaller than in *Euangelistes* but agrees in being simple and abruptly different from the molariform P_4. P_4 is very similar, with no true paraconid, large metaconid directly lingual to the protoconid, and well-developed, basined heel. There is a basal anterior cusp, but this is larger in *Metacodon* than in *Euangelistes. Ankylodon* is more like *Euangelistes* in this feature and, indeed, in P_4 as a whole. Both *Metacodon* and *Ankylodon* have M_{1-3} differing from *Euangelistes* only in minor details.

Resemblances in these simple cheek-tooth patterns may be misleading as to affinities, but it can at least be said that the synthetic Cretaceous form resembles *Metacodon* and, for the lower teeth, *Ankylodon* at least as much as any other described later genera. The time gap is great. Even if the resemblance were taken as conclusive of affinity, family reference would be uncertain, unless Butler's poorly based Metacodontidae were recognized, which I am not at present inclined to accept.

The most probable general interpretation at present seems to be that in the late Cretaceous and early Tertiary there was a complex of primitive insectivores with more or less erinaceomorph molars, all closely related as to ancestry but diverging in numerous minor lines. Some of these lines later became more distinctive and ramified in turn, including true Leptictidae and true Erinaceidae. Other lines in the complex died out early or continued for a time independently of well-defined later families. The syn-

thetic American Cretaceous insectivore belongs somewhere in the basal complex of this broad group, probably not in the direct ancestry of known later forms. *Metacodon* and *Ankylodon* perhaps represent an Oligocene survival from the same basic complex.

WORKS CITED

BUTLER, P. M.
1948. On the evolution of the skull and teeth in the Erinaceidae, with special reference to fossil material in the British Museum. Proc. Zool. Soc. London, vol. 118, pp. 446–500.

CLARK, J.
1937. The stratigraphy and paleontology of the Chadron formation in the Big Badlands of South Dakota. Ann. Carnegie Mus., vol. 25, pp. 261–350.
1939. Status of the Oligocene insectivore genus *Metacodon*. Jour. Paleont., vol. 13, pp. 139–140.

GREGORY, W. K., AND G. G. SIMPSON
1926. Cretaceous mammal skulls from Mongolia. Amer. Mus. Novitates, no. 225, pp. 1–20.

HALL, E. R.
1929. A second new genus of hedgehog from the Pliocene of Nevada. Univ. California Publ., Bull. Dept. Geol. Sci., vol. 18, pp. 227–231.

LULL, R. S.
1915. The mammals and horned dinosaurs of the Lance formation of Niobrara County, Wyoming. Amer. Jour. Sci., ser. 4, vol. 40, pp. 319–348.

MARSH, O. C.
1889a. Discovery of Cretaceous Mammalia. Amer. Jour. Sci., vol. 38, pp. 81–92.
1889b. Discovery of Cretaceous Mammalia. Part II. *Ibid.*, vol. 38, pp. 177–180.
1892. Discovery of Cretaceous Mammalia. Part III. *Ibid.*, vol. 43, pp. 249–262.

MATTHEW, W. D.
1916. A marsupial from the Belly River Cretaceous, with critical observations upon the affinities of the Cretaceous mammals. Bull. Amer. Mus. Nat. Hist., vol. 35, pp. 477–500.

OSBORN, H. F.
1891. A review of the Cretaceous Mammalia. Amer. Nat., vol. 25, pp. 595–611.
1893. Fossil mammals of the upper Cretaceous beds. Bull. Amer. Mus. Nat. Hist., vol. 5, pp. 311–330.
1898. Evolution of the Amblypoda, part I. Taligrada and Pantodonta. *Ibid.*, vol. 10, pp. 169–218.
1907. Evolution of mammalian molar teeth to and from the triangular type. New York and London, Macmillan Co.

PATTERSON, B., AND P. O. MCGREW
1937. A soricid and two erinaceids from the White River Oligocene. Field Mus. Nat. Hist., geol. ser., vol. 6, pp. 245–272.

SIMPSON, G. G.
1927. Mammalian fauna of the Hell Creek formation of Montana. Amer. Mus. Novitates, no. 267, pp. 1–7.
1928. Affinities of the Mongolian Cretaceous insectivores. *Ibid.*, no. 330, pp. 1–11.
1929a. American Mesozoic Mammalia. Mem. Peabody Mus. Yale Univ., vol. 3, i-xv, 1–235 pp.
1929b. Some Cretaceous mammals from the Lance formation. Ann. Carnegie Mus., vol. 19, pp. 107–113.
1932. The supposed occurrences of Mesozoic mammals in South America. Amer. Mus. Novitates, no. 530, pp. 1–9.

VIRET, J.
1940. Étude sur quelques erinacéidés fossiles (suite) genres *Plesiosorex*, *Lanthanotherium*. Trav. Lab. Géol. Fac. Sci. Lyon, mém. 28, fasc. 39, pp. 32–65.